

The University of Chicago

CASTE DETERMINATION AND DIFFER-  
ENTIATION, WITH SPECIAL REFER-  
ENCE TO THE GENUS RETICU-  
LITERMES (ISOPTERA)

A PART OF A DISSERTATION SUBMITTED TO  
THE FACULTY OF THE DIVISION OF THE  
BIOLOGICAL SCIENCES IN CANDIDACY FOR  
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOÖLOGY

1933

By  
LAURA HARE

Private Edition, Distributed by  
THE UNIVERSITY OF CHICAGO LIBRARIES  
CHICAGO, ILLINOIS

---

Reprinted from  
JOURNAL OF MORPHOLOGY  
Vol. 56, No. 2, 1934





The University of Chicago

CASTE DETERMINATION AND DIFFER-  
ENTIATION, WITH SPECIAL REFER-  
ENCE TO THE GENUS RETICU-  
LITERMES (ISOPTERA)

A PART OF A DISSERTATION SUBMITTED TO  
THE FACULTY OF THE DIVISION OF THE  
BIOLOGICAL SCIENCES IN CANDIDACY FOR  
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOÖLOGY

1933

By  
LAURA HARE

Private Edition, Distributed by  
THE UNIVERSITY OF CHICAGO LIBRARIES  
CHICAGO, ILLINOIS

---

Reprinted from  
JOURNAL OF MORPHOLOGY  
Vol. 56, No. 2, 1934

1800-1801

THE UNIVERSITY OF LEIDEN  
LIBRARY  
LEIDEN





## CASTE DETERMINATION AND DIFFERENTIATION WITH SPECIAL REFERENCE TO THE GENUS RETICULITERMES (ISOPTERA)

LAURA HARE

*Hull Zoölogical Laboratory, The University of Chicago*

FOUR PLATES (THIRTY-EIGHT FIGURES)

### AUTHOR'S ABSTRACT

The results of recent investigations concerning caste determination among termites have been briefly reviewed with emphasis upon the work of Thompson ('17). From examination of new data upon the development of *Reticulitermes arenicola* Goellner, *R. flavipes* (Kollar), and *R. tibialis* Banks, and of Thompson's original *R. flavipes* material, I am unable to substantiate her claim that the sterile and reproductive castes are separable into two distinct groups at the time of hatching. I could distinguish them first in stadium three and suggest that the second stadium may be a critical period in differentiation. From evidence to date, it must be granted that both intrinsic and extrinsic factors may play a role in the production of castes. The delay in appearance of demonstrable caste differences until the third stadium in the genus *Reticulitermes* at least admits of an opportunity for extrinsic factors to be effective. Growth and metamorphosis of various structures which ultimately lead to the three differentiated castes have been followed through successive stadia. Gynandromorphs and intercastes among social insects give indication of the physiological and genetic factors influencing both morphological and behavior differences among castes.

### INTRODUCTION<sup>1</sup>

The problem of interpreting the mechanism which underlies caste formation among termites has interested students of the social insects since the middle of the nineteenth century. Through a review of the work of recent investigators, particularly that of Thompson ('17), and the presentation of new data on the morphological aspects of differentiation in three species of the genus *Reticulitermes*, I have attempted, in the following pages to analyze critically the facts contributing to the present conflicting theories of caste formation and to indicate points where further research might be pertinent. Cases cited in which normal development has been modified parasitically, genetically, or environmentally, offer good material for both morphological and behavioristic analysis.

<sup>1</sup>I wish to express my sincere appreciation to Dr. A. E. Emerson for his suggestions and constructive criticism throughout the study, and to Dr. T. E. Snyder, through whose kindness Miss Thompson's original material was made available to me.

## HISTORICAL

In the search for an explanation of caste derivation, approaches have been made by direct observation and experimentation with diet, cross-breeding, histological examination, and a study of the effects of parasitism upon differential growth. Jucci ('24) stresses the importance of diet and believes that neoteinics are produced as the result of a special alimentary regime. Heath ('27, '31) and Kalshoven ('30), using species of the *Kalotermitidae*, likewise point to differential feeding and care, particularly in relation to the number of individuals in the colony, as the directing force in development. Weyer ('31), working primarily with *Nasutitermes* (= *Eutermes*) *amboinensis* (Kemner), suggests that the presence of quartz crystals among the eggs, causing unequal oxygenation, together with later care of the young, may influence the future course of differentiation into castes.

Representing the other school of thought, Thompson ('17, '19, '22) concluded that the sterile and reproductive castes could be distinguished at hatching by the larger size of the brain, reproductive organs, and compound eyes in the latter. Montalenti's ('29) investigations of *Reticulitermes lucifugus* (Rossi) appear to confirm her results regarding relative brain size but his material is insufficient to be conclusive. Imms ('19) strongly advocates genetic determination and Bathellier ('27), using *Macrotermes gilvus* (Hagen) and *Nasutitermes* (= *Eutermes*) *matangensis* (Haviland), claims he is able to distinguish all three castes at the time of hatching on a basis of the relative size of the reproductive organs. Growth during a stadium is proposed by him to account for differential brain size among the young forms. He suggests that temperature, humidity, and food may effect the germinal constitution of the parents.

A cytological study of the castes is rendered difficult because of the small size of the cells and the large number of chromosomes. Stevens ('05), working with the reproductive organs of male nymphs, determined the diploid chromosome number of *Zootermopsis* (= *Termopsis*) to be fifty-two.



Benkert ('30), using *Reticulitermes flavipes* material, reports forty-two chromosomes (diploid) in the reproductive male of the first form and has orally reported a similar number in the male soldier. Further investigation should determine whether or not the chromosome count is the same in all castes.

#### CASTE DETERMINATION AND MORPHOLOGY

My study of the early development has been carried out chiefly with *Reticulitermes arenicola* Goellner and the results checked with *R. flavipes* (Kollar) and *R. tibialis* Banks. Practically all of my material was collected from the Chicago area; *R. arenicola* and *R. tibialis* occur abundantly in the dunes along the southern shore of Lake Michigan, while *R. flavipes* is restricted to mesic conditions in this area. The fixatives used with best results were Van Leeuwen's and alcoholic Bouin. Staining in Conklin's picro-haematoxylin and clearing in cedarwood oil proved very satisfactory. Many of the specimens were mounted in balsam, others were kept in the cedarwood oil to facilitate orientation and dissection of the mandibles. Serial sections were made of eight individuals of the first instar to enable a more adequate study of the head structure. Measurements were made with an ocular micrometer under the 10x ocular with a 48-mm. objective. Several groups of termites were kept alive over long periods in the laboratory by being placed in finger bowls with moist paper toweling. Direct observation without disturbing was possible because their runways were made between the paper and the glass.

From large colonies, containing many eggs and young, the early development was studied and an attempt made to correlate my data with Thompson's ('17) *R. flavipes* material. She included within the first stadium the period from hatching until the young reach a total length of approximately 2.0 mm., subdividing it into early, middle and end phases. This admits of a gradual growth until practically double the initial size has been attained. She described the antennae as having nine initial joints, the third from the base minus

bristles, subsequently increasing to twelve joints, all bearing bristles, by the termination of the end phase. The earliest stage which I was able to find corresponds to her material labeled 'early phase,' but in neither case do the newly hatched young show nine antennal joints; ten is the initial number (figs. 11, 12). I could distinguish on a basis of size and antennal structure (pl. 3) the three groups which she included in the first stadium, but measurements of several structures (table 2 and fig. 1) indicate an increase in size which appears to me to require the acknowledgment of three separate stadia. I observed among my specimens the actual molting process of an individual from the second to the third stadium.

A study was made of the ratios of head width to brain (super-oesophageal ganglion) width to enable a statistical interpretation of this relationship. When these ratios of 150

TABLE 1

*Frequency scale of the head to brain width ratios in R. arenicola (first instar)*

| RATIO     | 1.07-1.08 | 1.09-1.10 | 1.11-1.12 | 1.13-1.14 | 1.15-1.16 | 1.17-1.18 | 1.19-1.20 | 1.21-1.22 | 1.23-1.24 | 1.25-1.26 | 1.27-1.28 | 1.29-1.30 | 1.31-1.32 |
|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| Frequency | 3         | 4         | 10        | 20        | 23        | 38        | 21        | 14        | 7         | 4         | 3         | 2         | 1         |

*R. arenicola* individuals of the first instar were plotted, a unimodal curve resulted in place of a subdivision into two distinct groups (table 1). Ninety-five first instar individuals of *R. flavipes* likewise failed to fall into two categories on this basis. Although certain individuals have markedly larger brains than others, transitional forms prevent a division into specific groups.

The size of the reproductive organs of forty-six *R. flavipes* females in the first stadium were carefully measured and the results compared with the respective head to brain width ratios in order to determine whether or not there exists a correlation of large gonads with low ratios. Of these forty-six there were thirteen contradictions to the above supposition and several inconclusive cases. *R. arenicola* also displays a considerable degree of variation in the size of the gonads with relation to head to brain width ratios.



Not until the third stadium could I segregate the sterile and fertile groups; at this time certain individuals show definite wing pad formation (fig. 5). The distance from the mid point of the anterior edge of the mesonotum diagonally back to the furthest point posterior shows a significant difference in the two groups; the average for those lacking pads is approximately 0.21 mm., for those with pads, 0.3 mm. Although the brain width is not distinctly smaller in the future sterile forms, the average ratio is 1.43 as compared to 1.36 for the reproductives (fig. 2). The greater head width of the sterile group at this time has a statistical significance of 0.0025 when examined by Students' method. The derivation and development of the second and third form reproductives is recognized as an important problem, but such a study could not be incorporated in the present work. The female reproductive organs, dissected out at this time and measured, showed a statistically significant difference; the average width in the sterile group was only 56 per cent of that of the wing pad group.

#### THE ROLE OF DIFFERENTIAL GROWTH IN CASTE FORMATION

The increase in size in successive stadia of the three castes was studied in order to understand more fully the growth processes which determine final morphological differences. The structures selected for comparative measurement are listed in table 2. As previously illustrated, the division into instars was made on a basis of antennal structure (pl. 3), wing pad development in the reproductives (pl. 3), and structural measurements (pl. 1). Some overlapping occurs in these measurements (table 2) but for the most part this is confined to the non-chitinous internal organs. Much overlapping of both internal and external measurements occurs in the fifth and sixth worker instars which thus are exceptions to the above statement. The sixth was considered a separate instar because of the additional antennal joints although possibly such a division is not valid.

Certain deductions from the study of the growth processes appear to be significant. The actual head width increases more rapidly in the worker-soldier group than in the fertile group, whereas, with respect to brain size, the converse is true. This difference is illustrated in figure 1, in the ratios of figure 2, and in figure 3 where the percentage of total increase in each stadium is graphically presented. A marked increase in the head length (measured to the anterior edge of the clypeus) of the immature soldier was noted (fig. 3), but perhaps the most striking example of differential growth is manifested by the mandibles (pl. 4). The appearance of the teeth in the worker and reproductive mandibles is practically identical until the sixth stadium when, in the left mandi-

TABLE 2  
Measurement of whole mounts of *R. arenicola*

| STADIUM                         | 1 (RWS)   | 2 (RWS)   | 3 (WS)    | 4 (WS)    | 5 (W)     | 6 (ADULT WORKER) |
|---------------------------------|-----------|-----------|-----------|-----------|-----------|------------------|
| Antennal joints                 | 10        | 12        | 12        | 14        | 15-16     | 17-18            |
| Total length (mm.)              | 0.85-1.43 | 1.40-1.87 | 1.69-2.37 | 2.38-3.03 | 3.06-4.26 | 3.38-4.14        |
| Head width (mm.)                | 0.30-0.39 | 0.44-0.50 | 0.57-0.66 | 0.72-0.84 | 0.87-0.99 | 0.93-0.98        |
| Brain width (mm.)               | 0.25-0.35 | 0.32-0.39 | 0.39-0.46 | 0.46-0.53 | 0.54-0.62 | 0.57-0.63        |
| Pronotum width (mm.)            | 0.19-0.25 | 0.28-0.32 | 0.32-0.40 | 0.41-0.51 | 0.57-0.71 | 0.61-0.74        |
| Femur + trochanter length (mm.) | 0.19-0.24 | 0.31-0.35 | 0.40-0.47 | 0.52-0.58 | 0.66-0.79 | 0.74-0.81        |
| Left mandible (a-b) (mm.)       | 0.12-0.15 | 0.18-0.21 | 0.23-0.28 | 0.30-0.35 | 0.37-0.43 | 0.40-0.44        |
| Left mandible (a-d) (mm.)       | 0.13-0.15 | 0.17-0.21 | 0.24-0.28 | 0.29-0.33 | 0.36-0.40 | 0.38-0.39        |
| Individuals measured            | 150       | 177       | 52        | 50        | 70        | 15               |

| STADIUM                         | 3 (R)     | 4 (R)     | 5 (R)     | 6 (R)     | 7 (R)     | 8 (ADULT REPRODUCTIVE) |
|---------------------------------|-----------|-----------|-----------|-----------|-----------|------------------------|
| Antennal joints                 | 12        | 14        | 15-16     | 17        | 17-18     | 17 <sup>1</sup>        |
| Total length (mm.)              | 1.75-2.33 | 2.68-3.44 | 3.11-3.57 | 4.08-5.02 | 4.41-5.52 | 4.25-5.19              |
| Head width (mm.)                | 0.56-0.63 | 0.72-0.76 | 0.82-0.86 | 0.87-0.93 | 0.89-0.95 | 0.81-0.86              |
| Brain width (mm.)               | 0.39-0.46 | 0.50-0.56 | 0.58-0.61 | 0.60-0.70 | 0.66-0.73 | 0.61-0.66              |
| Pronotum width (mm.)            | 0.36-0.40 | 0.50-0.53 | 0.60-0.66 | 0.65-0.77 | 0.69-0.79 | 0.67-0.74              |
| Femur + trochanter length (mm.) | 0.42-0.47 | 0.56-0.58 | 0.63-0.68 | 0.72-0.77 | 0.75-0.82 | 0.81-0.86              |
| Left mandible (a-b) (mm.)       | 0.23-0.26 | 0.30-0.31 | 0.33-0.35 | 0.35-0.39 | 0.36-0.40 | 0.39-0.42              |
| Left mandible (a-d) (mm.)       | 0.22-0.25 | 0.29-0.30 | 0.32-0.33 | 0.35-0.37 | 0.32-0.37 | 0.35-0.39              |
| Individuals measured            | 72        | 4         | 8         | 27        | 35        | 30                     |

(RWS), indistinguishable stage; (WS), worker-soldier nymph; (R), reproductive nymph; (W), worker nymph.

<sup>1</sup> One individual showed the coalescence of joint 15 and 16 of the nymph, forming joint 15 of the adult. (The antennal joints are numbered from the distal extremity to the base.)



ble of the latter group, a small tooth appears proximal to the third (fig. 38). In the transformation undergone to produce the immature soldier a center of rapid growth originates between the third and fourth teeth which causes a lengthening from the base to the distal tip. The second and third teeth of the worker mandible, in a reduced form, are apparently pushed out toward the tip during this process while the fourth tooth remains near the large basal tooth (figs. 27, 31). An indication, occasionally, of a much reduced tooth between the third and fourth, in the left mandible, is possibly homologous with the one in the reproductive caste (fig. 38). Toward the end of this stadium the preformed mature soldier mandible can be seen clearly outlined and an attempt was made to homologize the teeth (fig. 28). It seems plausible that in the mature left mandible the second and third teeth have disappeared completely, the fourth tooth is replaced by a series of three shallow teeth, and the small spine-like tooth just distal to the basal tooth of the mature mandible forms as a separation from the bulk of this basal tooth. Similarly, an attempt was made to homologize the teeth of the right mandibles of worker, immature, and adult soldier (figs. 30 to 32). The rounded second and more prominent third teeth of the worker and young soldier are lost in the adult, and the fourth tooth of the worker appears to have remained near the basal ridged portion during the elongation process and is only faintly recognizable in the adult. The origin of the rather prominent tooth at the distal end of the molar surface is doubtful, but possibly it forms as a rapidly growing portion of that surface.

#### OBSERVATIONS OF ECDYSIS

From collections made in late fall and early spring, evidence indicated that large numbers of *R. arenicola* first form reproductives pass the winter in the sixth stadium. Logs were brought into the laboratory the first of April and the termites removed to finger bowls for further observation. About 2 weeks later practically all of them had molted (within a period

of 3 days) into the seventh stadium in which they remained until the latter part of May. Flight of *R. arenicola* occurs later than in the other two species, taking place late in May through June and early July.

In a group of *R. flavipes* collected at Valparaiso, Indiana, and kept through the winter in the laboratory, immature soldiers, molting from worker-like forms, appeared about the first of April and at frequent intervals throughout the spring. These individuals could be distinguished by their more elongated heads and enlarged mandibles (fig. 24), the latter pigmented at the tips. The duration of this immature soldier stadium was quite constant in a number of carefully checked cases, lasting 17 to 19 days. The adult soldiers, upon emergence, have colorless heads. Three to 4 days are required for the manifestation of the mature brownish pigmentation. *R. tibialis* individuals were observed undergoing a similar development. From the fact that the immature *R. flavipes* soldiers differed markedly in size, and the adult soldiers (17) varied as much as 1.07 to 1.36 mm. for the head width and 1.77 to 2.19 mm. for head length, possibly the immature soldiers molt from different instars of the worker-like nymphs.

#### DISCUSSION

It would seem, from an analysis of recent investigations, that any theory of caste formation among termites must incorporate the possibility of both original genetic determination and the influence of extrinsic factors. Among the latter should be included differential care and feeding (correlated with size of colony), temperature, and other climatic conditions, acting upon the parents or the young or possibly upon both.

Bathellier ('27), from observations upon termites of Indo-China, noted a rhythm in the production of eggs which later developed into reproductive individuals, and suggests that it may be correlated with seasonal changes. Among tropical termites, where cold winter temperature cannot be a determining influence, flying nevertheless occurs at more or less



definite times for each species. This indicates a similar rhythmic cycle, associated in the tropics with the dry and rainy seasons. The temperate *Reticulitermes* genus in the Chicago area has its flight regularly in the spring and early summer, although exceptional appearances of winged forms in the fall and winter have been recorded. Judging the average length of a stadium to be approximately a month, a monthly census of the population within termite colonies of the same locality should produce valuable data. If there is any degree of lability in the type of eggs which the queen may lay, it is feasible to grant that general metabolism, closely associated with the reproductive function, may in turn be correlated with food, temperature, and moisture conditions.

The conclusion of Bathellier ('27) that the three castes can be distinguished at hatching by differential size of the reproductive organs could not be substantiated by Weyer's ('31) or my own observations. Because of the delicacy of these structures in the early stages and the possibility of confusing the two sexes (these organs are more moniliform in the male) it would appear that this character is too variable to prove an adequate indicator of the future castes. Great care must be taken in the interpretation of material distorted by fixation. In individuals just prior to or immediately following ecdysis, whereas the outer chitin maintains its normal dimensions, the inner tissues may shrink away, leaving a transparent area in between. The head, thus modified, shows a distortion of the brain; the mandibular muscles, pulled away from the outer capsule, cause a lateral compression of the two lobes and a false impression of relative size is given.

Unfortunately, Thompson ('17) gives no tables of structural measurements of a statistical nature to substantiate her assertions. I have examined her *R. flavipes* material and to the best of my knowledge her observations were made upon the following material:

For the 'early phase' there are fourteen specimens labeled worker-soldier type, two sex type (reproductive), and thirty unlabeled.

For the 'middle phase' there are fifteen specimens labeled worker-soldier type, seventeen sex type (five with a question mark), and one unlabeled.

For the 'end phase' there are seven specimens labeled worker-soldier type (two with a question mark), eight sex type (two with a question mark), and seven unlabeled.

Approximately 35 per cent of this material is in a poor state of preservation due to distortion from mounting.

There are serial sections of fifteen 'early phase' individuals for her study of the differential size of the compound eyes, but most of this material is inadequate for cellular detail. In only three cases are the compound eyes clearly defined. She stated that the frontal gland, although barely recognizable, is more differentiated in the reproductive than in the sterile group at the time of hatching, but the actual material from which her figures are drawn comprised the only examples I could find.<sup>2</sup>

Obvious discrepancies exist between her observations and my own, both in the designation of stadia and in the determination of the time at which the sterile and fertile castes become distinguishable. From my data, one should expect

<sup>2</sup>I also had an opportunity, through the kindness of Doctor Snyder, to examine the material referred to in Thompson's ('19) later paper. With regard to thirteen separate species she claimed to have distinguished the fertile from the sterile caste at hatching by the larger size of the brain and reproductive organs and usually more opaque body of the former. The material, adequately preserved for analysis, included the following young forms (probably first stadium):

Zootermopsis (Termopsis) angusticollis, 3 labeled soldier, 6 reproductive (1 with a question mark), and 10 unlabeled; Neotermes castaneus (nymphs 1.8 to 2.1 mm.), 5 labeled soldier, 4 reproductive, and 3 unlabeled; Kalotermes n. sp. Banks, 5 labeled soldier (4 in poor condition and 1 with a question mark) 14 reproductive (12 in poor condition and 3 of these with a question mark); Cryptotermes cavifrons, 2 labeled soldier, 1 reproductive; Reticulitermes virginicus, 7 labeled worker-soldier, 4 reproductive, and 23 unlabeled; Arrhinotermes simplex, 2 labeled worker-soldier, 15 unlabeled; Nasutitermes (Eutermes) pilifrons, 22 unlabeled; N. morio, 3 unlabeled; N. sanchesi, 8 unlabeled; Anoplotermes fumosus, 2 unlabeled; Amitermes tubiformans, 4 unlabeled.

The large number of specimens with type not designated or with designation followed by a question mark makes the validity of her separation at this stage into two distinct groups questionable.



to find the first indications in the second stadium of certain individuals showing characteristics of the sterile or fertile caste. Among numerous individuals of this developmental stage a semblance of wing pad formation is occasionally recognizable, and the coefficient of correlation of brain and reproductive organ width was 0.318 for ninety-five *R. arenicola* females. This might be interpreted as a foreshadowing of certain distinctions manifested in the third stadium.

Thompson's ('17) supposition concerning three phases of growth within the first stadium of *R. flavipes* raises a question, namely, can the non-flexible chitin (such as sclerites and head capsule) expand to the point of doubling in size without the intervention of a molt? Investigators have studied this problem of growth with a variety of insects and other arthropods. Eidmann ('24) worked with *Dixippus morosus*, *Periplaneta americana*, *Tenebrio molitor*, and *Libellula quadrimaculata*; Titschack ('24) with *Carausius* (*Dixippus*) *morosus* and *Tineola biselliella*; Teissier ('28) with *Dixippus morosus* and *Notonecta glauca*; and Przibram ('31) with *Sphodromantis* (*Hierodudula bioculata*, *Tenodera aridifolia*, five additional mantid species, Ostracoda and Decapoda. The conclusions reached indicate that at the time of each molt the weight is approximately doubled, while the linear measurement of length is increased 25 to 35 per cent. Eidmann ('24) says:

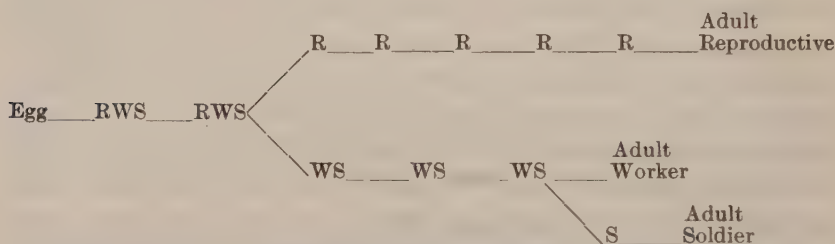
Wir sehen demnach jede Formveränderung des Insektenkörpers, sei sie nun mit Wachstum vereinigt oder nicht, notwendig an eine Häutung gebunden. Der Grund dafür ist wieder der, dass die Chitinschicht, weil ohne eigenes Leben, nicht mehr umbildungsfähig ist.

These data, if applicable to termites, lend support to my decision to subdivide Thompson's ('17) first stadium into three separate stadia.

Although Grassi and Sandias (1896-1897), Bugnion ('13), Imms ('19), and certain others maintain that external antennal structure is modified irrespective of molting, I am inclined to the view of Fuller ('20), namely, that any joint modi-

fication occurs coincident with molting. The constancy of the antennal appearance within stadia seems further to substantiate this hypothesis.

The total number of molts undergone by each caste differs unquestionably among species, the primitive termites having more stadia than the highly specialized species. Heath ('31) shows 9 stadia occurring in *Zootermopsis*. My estimate for *Reticulitermes* is 8 stadia for the first form reproductives, 6 or 7 for the soldiers, and 5 or 6 for the workers. Bathellier's ('27) determination for *Nasutitermes matangensis* is 7 for the reproductives, 5 for the soldiers, and 4 for the workers. Even within a species the numbers are not constant but depend upon food and climatic conditions. Following is a scheme of the stadia as deduced from my observations of three *Reticulitermes* species.



Explanation: RWS, indistinguishable stage; WS, worker-soldier nymph; R, reproductive nymph; W, worker nymph; S, soldier nymph.

Judging the duration of stadia from observed cases to be approximately a month (time of extreme cold excepted), the first form reproductives should reach the adult condition in a little over a year.

Emerson ('26) presents evidence for the phylogenetic origin of the soldier caste from the first form reproductives. Subsequent specialization of the soldier has brought about mandibular modifications and loss of fertility. Since the soldier molts from a worker-like form (observed many times), these two sterile castes must be derived from a common stem which at some time separates from the reproductive line. According to my observations, this primary separation has oc-



curred by the third stadium; the workers and soldiers become distinguishable from each other at a later molt. The fact that my conclusions point to a later differentiation than determined upon by Thompson ('17, '19) does not alter the hypothesis that the worker is phylogenetically a neotonous soldier rather than a direct derivation from any of the reproductive types.

Each of the three castes presents a distinct picture with respect to the morphological aspect of growth in successive stadia. In the structures of the worker termite a rather symmetrical growth occurs, although extreme specialization is shown in the lack of functional compound eyes and functional reproductive organs. The first form reproductives attain long pairs of wings which are shed shortly after emergence from the colony and a further remarkable feature, not described here, is the degrees to which the abdomens of mature females are able to expand, particularly those of the specialized tropical species. The modifications undergone by the soldier caste are perhaps most striking. The immature soldier molts from a worker-like skin to display an enlarged head and elongated mandibles. The transformation of the worker-type mandible to that of the adult soldier has been discussed and is illustrated (pl. 4) for *Reticulitermes*.

A comparison of the mandibular growth in this genus with that in *Archotermopsis*, *Hodotermopsis*, and *Zootermopsis* (Emerson, '33) indicates that in the latter a different type of morphological differentiation takes place. In the case of the genera of the primitive subfamily *Termopsinae* the mandible shows the same number and arrangement of teeth in the nymph and in the adult soldier without degeneration of certain teeth.

The excessive growth in specific regions of the mandibles can be explained by Huxley's ('32) theory of positive heterogony. The new growth center appears following the molt from worker-like individual to soldier, and is determined genetically by specific rate-controlling genes. Prior to this molt, which might be interpreted as marking a threshold,

these genes were unable to function in such a capacity. The origin and control of regions possessing a high growth increment appears to be closely associated with a physiological balance which may be upset by such an abnormal phenomenon as parasitism. In this connection the discovery by Silvestri ('26) of soldiers of *Macrotermes* (= *Termes*) *gilvus* (Hagen), parasitized in the head by larvae of *Conopidae*, seems pertinent. These individuals show many characters intermediate between soldier and worker but retain the worker-like mandibles which indicates that parasitism must have occurred prior to the transforming molt. According to Silvestri's interpretation a salivary secretion of the parasite causes histolysis of the mandibular muscles and prevents the typical soldier mandible from becoming manifest.

Wheeler ('28 a), in a study of ants infected with nematodes of the genus *Mermis*, presents comparable cases of individuals displaying a combination of soldier, worker, and female characters. Wheeler interprets these mermithergates as an indication of a high degree of instability among ants since certain grasshoppers and *Diptera*, similarly parasitized, remain morphologically unmodified. This fact has contributed to his theory that among ants all fertilized eggs have the same genetic constitution. Wheeler ('33) states that behavior differences in the worker and female are largely phenotypic, controlled by the condition of the reproductive system; the neural endowment is the same in both castes. In contrast, Tulloch ('32), from examination of a gynergate *Myrmecia* (*Promyrmecia*) *aberrans* Forel in which the right side resembles a female and the left side resembles a worker, concludes that here is evidence favoring the germinal hypothesis of caste determination among ants. All gynandromorphs previously described showed a combination of male and female characters which had been interpreted as supporting the trophogenic hypothesis.

No cases of gynandromorphs or intersexes have ever been found among termites. Heath ('28) reports the frequent occurrence of intercastes in the form of fertile soldiers in the



genus *Zootermopsis* (= *Termopsis*). Females of this type with soldier mandibles and functional ovaries show behavior responses similar to the complemental royal forms.

Whereas among vertebrates behavior and secondary sexual characters are correlated with sex hormones, to quote from Whiting ('32): "In insects, on the other hand, it has long been observed that character of the various body regions is determined locally and, in any case, independently of gonads." Whiting ('32) has shown from his work with *Habrobracon juglandi* that among sex mosaics (gynandromorphs) the reactions of an individual are governed by the head, regardless of the sex of the abdomen. Similar types of *Drosophila* gynandromorphs, which corroborate the above statement, have been reported. It therefore appears that the induction of behavior responses must be determined for each type of morphological abnormality with adequate control upon the physiological effects of the gonads, and upon hereditary influences.

Each termite caste is normally characterized by specific inherited behavior responses. Thus the workers and immature forms are primarily concerned with the construction of the nest and the care of the young, the soldiers act in a protective capacity, and upon the reproductives falls the responsibility of founding and perpetuating the colony.

Just what it is that brings about caste differences can at present only be surmised. Centers of rapid and of inhibited growth are possibly induced by special rate-controlling genes which are able to act only beyond a specific threshold. But whether the realization of this threshold is genetically determined or is influenced by extrinsic factors or whether both play a part, still remains an unanswered problem.

## CONCLUSIONS

1. Three separate stadia after hatching are recognized in place of three growth phases, comprising a single stadium, as reported by Thompson ('17).

2. The sterile caste is distinguished from the fertile caste in stadium 3.

3. Stadium 2 is suggested as a critical period in differential development.

4. Development in the first form reproductives produces long wings, a relatively enlarged brain, functional gonads, and compound eyes.

5. The worker develops a relatively enlarged head capsule (with smaller brain), functionless gonads, and reduced compound eyes.

6. Two molts are required to produce an adult soldier from a worker-like individual of the fifth (?) instar.

7. Homologies of the mandibular teeth of the worker-type, soldier nymph, and adult soldier are suggested.

8. The region of growth during the development of the soldier mandible differs in *Reticulitermes* compared to the *Termopsinae*.

9. On the basis of known facts it is impossible theoretically to exclude either intrinsic or extrinsic factors from playing a role in caste determination.

10. Evidence from collection records indicates that there is a cyclic rhythm in the production of fertile forms which possibly is correlated with climatic conditions.



## LITERATURE CITED

- BATHELLIER, J. 1927 Contribution à l'étude systematique et biologique des termites de l'Indochine. Faune des Colonies Francaises, Paris, T. 1, pp. 121-365.
- BENKERT, J. H. 1930 Chromosomal study of *Reticulitermes flavipes*. Proc. Pa. Acad. Sc., vol. 4, pp. 1-3.
- BUGNION, E. 1913 La differentiation des castes chez les termites. Bull. Soc. Ent. France, no. 8, pp. 213-218.
- EIDMANN, H. 1924 Untersuchungen über Wachstum und Häutung der Insekten. Zeit. f. Morph. u. Ökol. der Tiere, Bd. 2, S. 567-610.
- EMERSON, A. E. 1926 Development of a soldier of *Nasutitermes* (*Constrictitermes*) *cavifrons* (Holmgren) and its phylogenetic significance. Zoologica, vol. 7, pp. 69-100.
- 1933 A revision of the genera of fossil and recent Termopsinae (Isoptera). U. of Cal. Publ. Ent., vol. 6, pp. 165-196.
- FULLER, C. 1920 Studies on the post-embryonic development of the antennae of termites. Ann. Natal Mus., vol. 4, pp. 235-295.
- GOELLNER, E. J. 1931 A new species of termite, *Reticulitermes arenincola*, from the sand dunes of Indiana and Michigan, along the shores of Lake Michigan. Proc. Ent. Soc. Wash., vol. 33, pp. 227-234.
- GRASSI, B., AND A. SANDIAS 1896-1897 Constitution and development of termites. Quart. J. Micros. Sc., vols. 39-40, pp. 245-322, 1-75.
- HARRIS, J. A., C. M. JACKSON, D. G. PATERSON AND R. E. SCAMMON 1930 The measurement of man. U. of Minn. Press.
- HEATH, H. 1927 Caste formation in the termite genus *Termopsis*. J. Morph., vol. 43, pp. 387-425.
- 1928 Fertile termite soldiers. Biol. Bull., vol. 54, pp. 324-326.
- 1931 Experiments in termite caste development. Science, vol. 73, p. 431.
- HEATH, H., AND B. C. WILBUR 1927 The development of the soldier caste in the termite genus *Termopsis*. Biol. Bull., vol. 53, pp. 145-154.
- HUXLEY, J. S. 1932 Problems of relative growth. London: Methuen & Co., Ltd.
- IMMS, A. D. 1919 On the structure and biology of *Archotermopsis*, together with descriptions of a new species of intestinal protozoa and general observations on the Isoptera. Phil. Trans. Roy. Soc. London (B), vol. 209, pp. 75-180.
- JUCCI, J. C. 1920 Sulla differenziazione della caste nella societa dei Termitidi i neotenici. Rend. del. R. Accad. Naz. Lincei (Anno CCCXVII), vols. 29, 30, ser. 5, 20.
- 1924 Su la differenziazione de la caste nella societa dei Termitidi. Reale Accad. Naz. Lincei (Anno CCCXX, 1923), Roma, vol. 14, ser. 5.
- KALSHOVEN, L. G. E. 1930 De Biologie van de Djatitermiet (*Kalotermes tectonae* Damm.) in Verband met zijn Bestrijding.
- MONTALENTI, G. 1929 Sul differenziamento delle caste nel *Termes lucifugus*. Boll. Ist. di Zool. della R. Univ. di Roma, vol. 7, pp. 1-23.
- PRZIBRAM, H. 1931 Connecting laws in animal morphology. U. of London Press, Ltd.

- PRZIBRAM, H., AND L. BRECHER 1930 Wachstumsmessungen an *Tenodera ardifolia* Stoll., einer Japanischen Fangheuschrecke. Arch. f. Entw.-mech. Org., Berlin, Bd. 122, S. 251-279.
- SILVESTRI, F. 1926 Descrizione di particolari individui (*Myia genii*) di *Termes gilvus* Nag. parassitizzati da larva di Dittero. Boll. Lab. Zool. Gen. Agrar. Portici, vol. 19, pp. 1-18.
- SNYDER, T. E. 1913 Changes during quiescent stages in the metamorphosis of termites. Proc. Ent. Soc. Wash., vol. 15, pp. 162-165.
- 1915 Biology of the termites of the eastern United States, with preventive and remedial measures. U. S. Dept. Agric., Bur. Ent. Bull. no. 94, pp. 13-95.
- 1925 The origin of the castes in termites. Proc. Biol. Soc. Wash., vol. 38, pp. 57-68.
- 1926 The biology of termite castes. Quart. Rev. Biol., vol. 1, pp. 522-552.
- SNYDER, T. E., AND E. P. POPENOE 1932 The founding of new colonies by *Reticulitermes flavipes* Kollar. Proc. Biol. Soc. Wash., vol. 45, pp. 153-157.
- STEVENS, N. M. 1905 Studies in spermatogenesis, with special reference to the 'accessory chromosome.' Carnegie Inst. Wash. Publ. 36, pp. 1-32.
- TEISSIER, T. G. 1928 a Croissance ponderale et croissance lineaire chez les Insectes. C. R. Soc. de Biol., T. 98, pp. 842-844.
- 1928 b Sur les dysharmonies de croissance chez les Insectes. C. R. Soc. de Biol., T. 99, pp. 297-299.
- THOMPSON, C. B. 1917 Origin of the castes of the common termite, *Leucotermes flavipes* Kollar. J. Morph., vol. 30, pp. 83-153.
- 1919 The development of the castes of nine genera and thirteen species of termites. Biol. Bull., vol. 36, pp. 379-398.
- 1922 The castes of *Termopsis*. J. Morph., vol. 36, pp. 493-535.
- THOMPSON, C. B., AND T. E. SNYDER 1919 The question of the phylogenetic origin of termite castes. Biol. Bull., vol. 36, pp. 115-132.
- TITSCHAK, E. 1924 Untersuchungen über das Wachstum, den Nahrungsverbrauch und die Eierzeugung. Zeit. wiss. Zool., Bd. 123, S. 431-487.
- 1926 Ibid., Bd. 128, S. 509-569.
- TULLOCH, G. S. 1932 A gynergate of *Myrmecia*. Psyche, vol. 39, pp. 48-51.
- WEYER, F. 1931 Das Problem der Kastendifferenzierung bei den Termiten. Biol. Zentralbl., Bd. 51, S. 353-373.
- WHEELER, W. M. 1928 a Mermis parasitism and intercastes among ants. J. Exp. Zool., vol. 50, pp. 165-237.
- 1928 b The social insects, chaps. 6, 7, pp. 130-220. New York: Harcourt, Brace & Co.
- 1933 Colony-founding among ants. Harvard U. Press.
- WHITING, P. W. 1932 Reproductive reactions of sex mosaics of a parasitic wasp, *Habrobracon juglandis*. J. Comp. Psych., vol. 14, pp. 345-363.

PLATES



## PLATE 1

### EXPLANATION OF FIGURES

1 Growth in millimeters in succeeding stadia of *R. arenicola*. I, indistinguishable stage; ♀, worker; R, first form reproductive.

2 Graphic representation of the ratio of head width to brain width in *R. arenicola*. 2f, soldier.

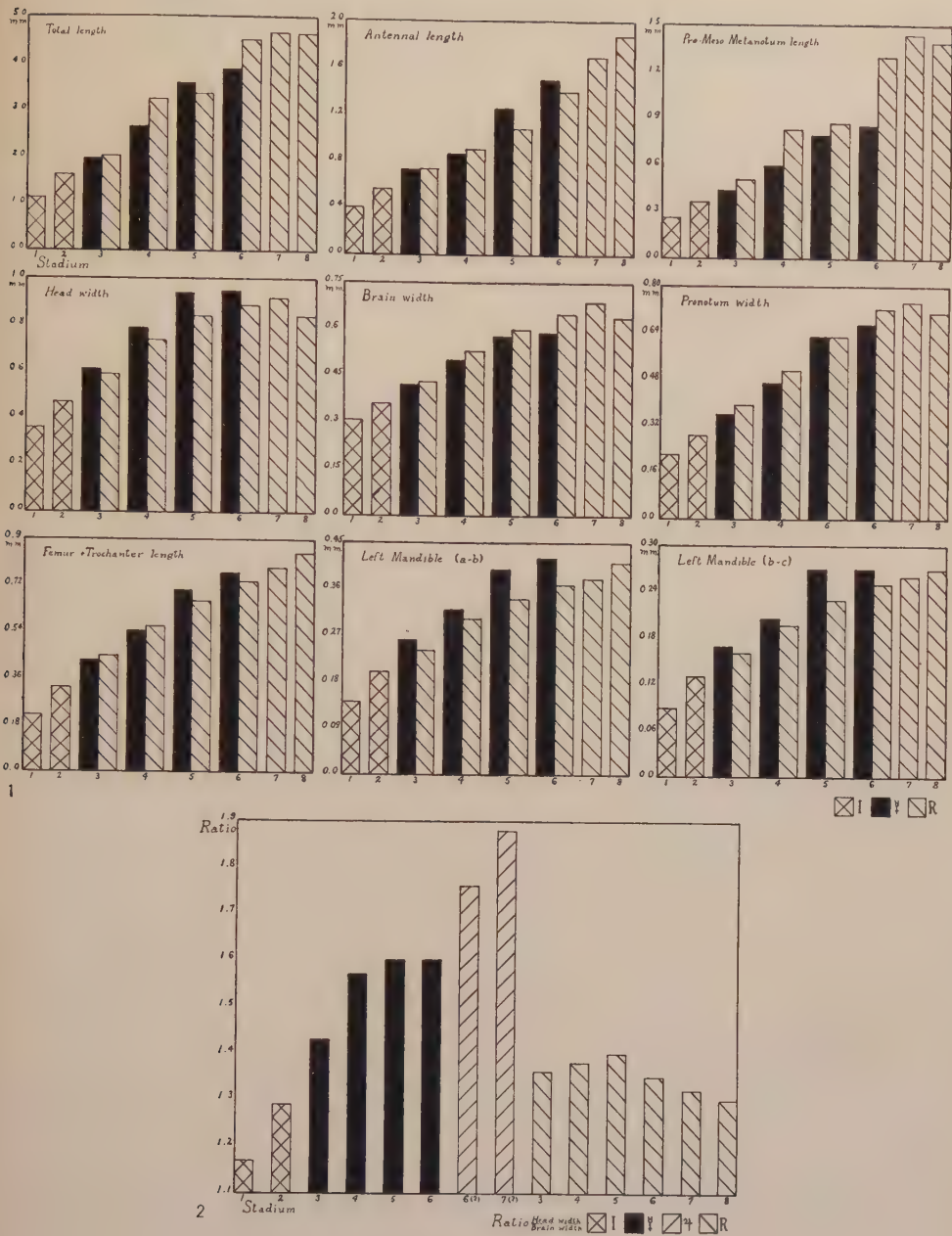
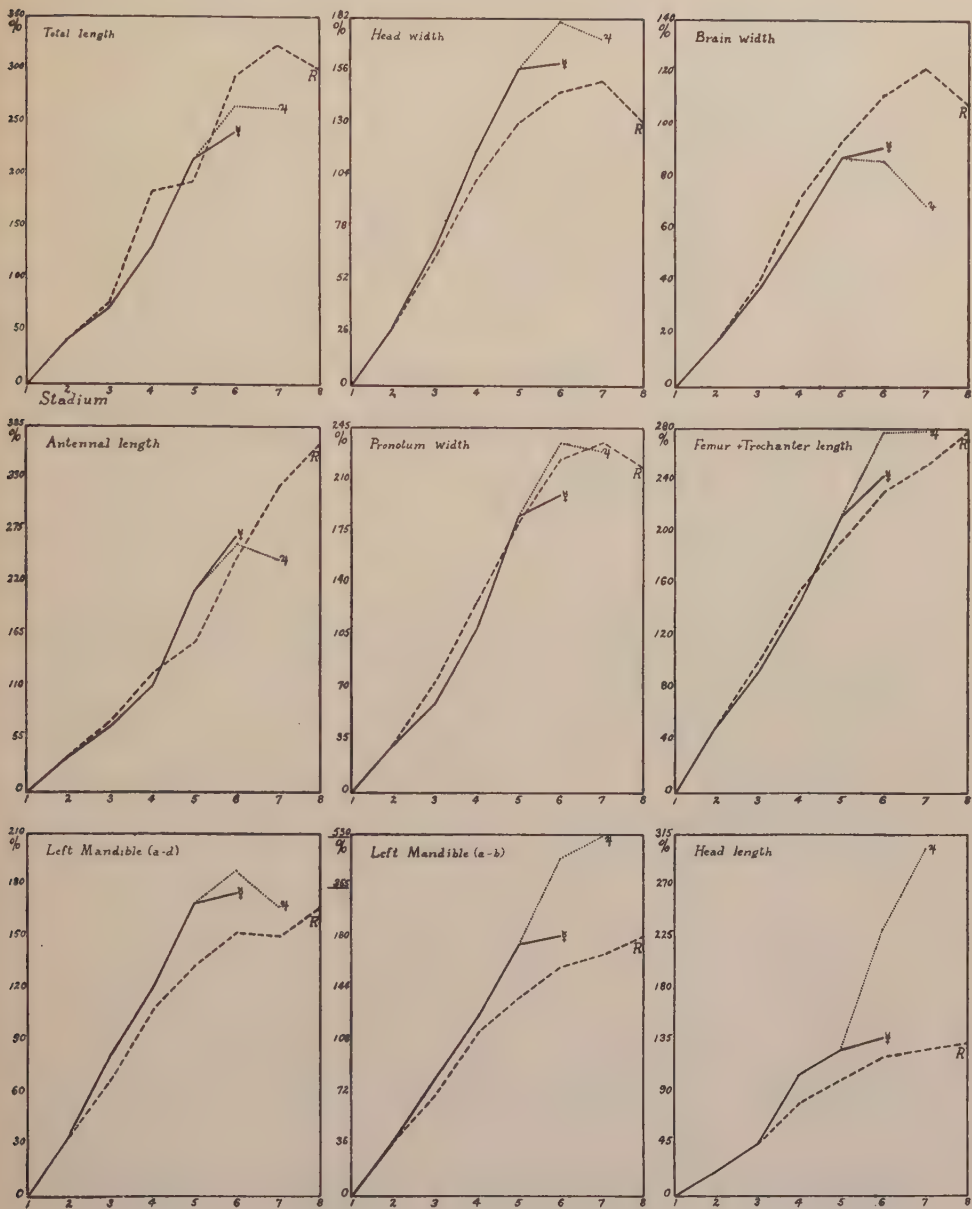


PLATE 2

EXPLANATION OF FIGURE

3 Total per cent of growth in succeeding stadia of *R. arenicola*. R, first form reproductive; ♀, worker; ♂, soldier.



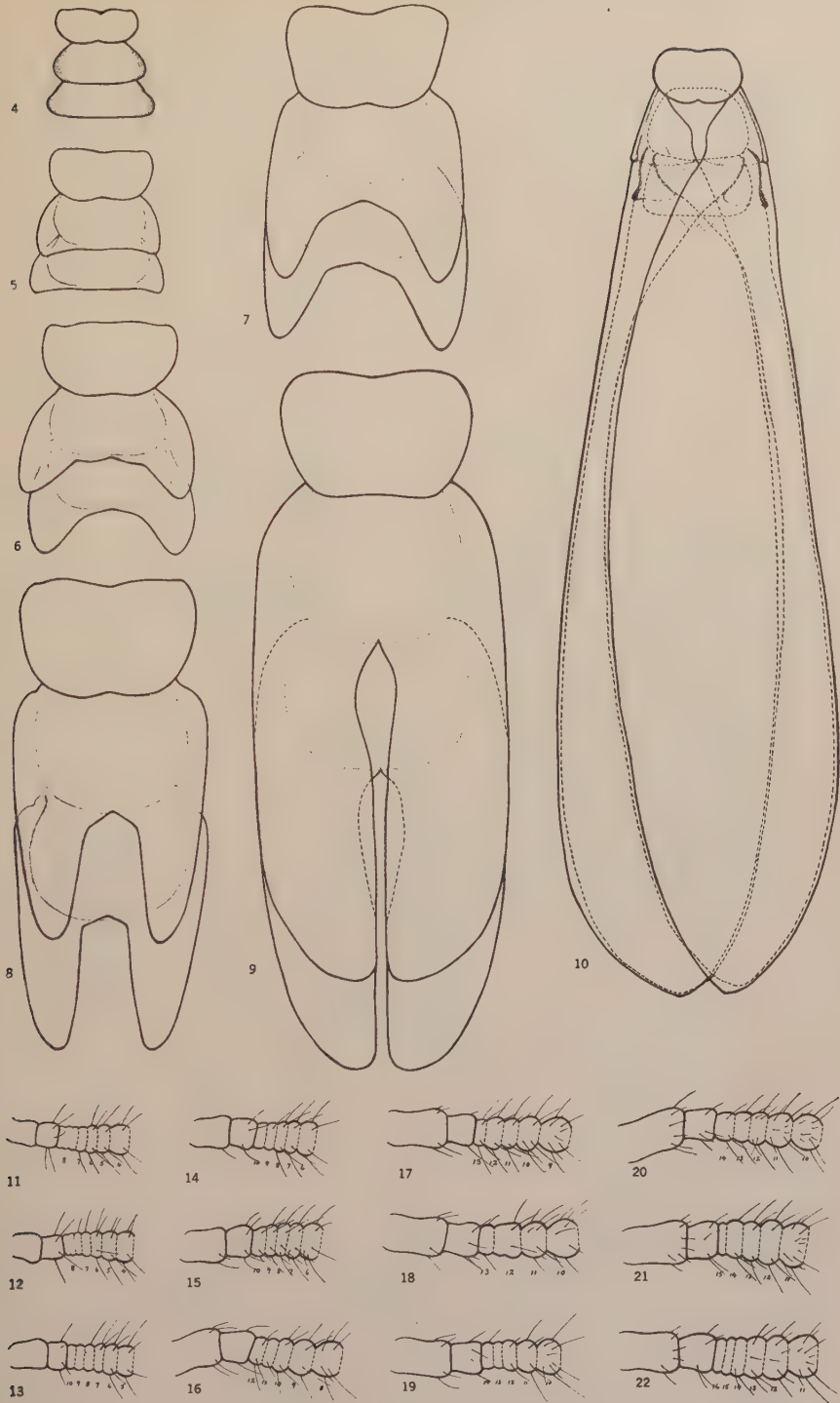


### PLATE 3

#### EXPLANATION OF FIGURES

Camera lucida drawings of wing pad development in the first form reproductives of *R. arenicola*.

- 4 Second instar (indistinguishable stage).
- 5 Third instar.
- 6 Fourth instar.
- 7 Fifth instar.
- 8 Sixth instar.
- 9 Seventh instar.
- 10 Imago. Camera lucida drawings of proximal antennal joints numbered basally from the tip. (No distinction noted between antennae of reproductive and sterile castes until sixth instar.)
- 11 and 12 First instar.
- 13 and 14 Second instar.
- 15 Third instar.
- 16 Fourth instar.
- 17 to 20 Fifth instar.
- 21 and 22 Sixth instar (fig. 22, worker caste).





## PLATE 4

### EXPLANATION OF FIGURES

Camera lucida drawings of *R. arenicola*.

- 23 Worker head.
- 24 Immature soldier head.
- 25 Soldier head.
- 26 Left mandible of worker.
- 27 Left mandible of immature soldier.
- 28 Left mandible of immature soldier (ventral).
- 29 Left mandible of soldier.
- 30 Right mandible of worker.
- 31 Right mandible of immature soldier.
- 32 Right mandible of soldier.
- 33 Left mandible of first instar.
- 34 Left mandible of second instar.
- 35 Left mandible of third instar (worker-type).
- 36 Left mandible of fourth instar (worker-type).
- 37 Left mandible of fifth instar (worker-type).
- 38 Left mandible of sixth instar (reproductive, ventral).









